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THE BREEDING HABITS OF THE RAINBOW DARTER (*ETHEOSTOMA CÆRULEUM* STORER), A STUDY IN SEXUAL SELECTION.

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Contributions from the Zoölogical Laboratory of the University of Michigan. No. 113.

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I. INTRODUCTION.

The brilliant coloration of the rainbow darter has been frequently mentioned since its first description by Storer (1845). It has given the fish its name and its reputation as perhaps the gaudiest of American fresh-water fishes (Jordan and Everman, 1896). The bright colors are present, however, only in the male so that there is marked sexual dimorphism. A similar condition exists, so far as I can learn, in all the closely allied forms of darters, each showing a characteristic color pattern. In addition to this the males of each of the many species show in the breeding season a more intense coloration. In the spring of 1906 I discovered this *Etheostoma* breeding under conditions favorable for close observation, and undertook the following study in order

to learn if possible whether any relation could be found between the behavior and the color characters. The work was carried on under the supervision of Professor Jacob Reighard to whom I am indebted for many suggestions.

The only published account that I have been able to find of the breeding habits of the darters is a brief notice by Seal (1897) who observed *Boleosoma olmstedii* and *Etheostoma caeruleum* in the Washington Aquarium. The rainbow darters observed by Seal were probably not kept under normal conditions for spawning, for in an aquarium the water is usually too deep, there is no current, and the available spawning area is small. My own observations were made in Mallet Creek about three miles east of Ann Arbor, Mich., where the stream is three to six feet across and forms a succession of shallow rapids and deep pools, varying in depth from two inches to two feet.

II. USUAL APPEARANCE, HABITAT, AND BEHAVIOR OF THE FISH.

Etheostoma caeruleum seldom exceeds two and one half inches in length, including the caudal fin. Among the fish examined there was little difference in the size of the two sexes, although a few males of three inches were found while no female reached that length. The colors of both sexes are described by Jordan and Everman (1896) and other systematic writers.

The colors of the female only slightly change with age or season and are like the sand or the gravel upon which the fish rests. There is on the back and sides a background of tan or olive with brown or blackish patches. On the anterior part of the body these are small, indefinite, and irregularly placed, but along the lateral line they are closer together elongated, and obliquely directed. Near the front edge of the second dorsal they merge into transverse bars which are more distinct below the caudal part of the lateral line. There are usually five of these. The last bar has a projection backward which separates two light brown spots at the base of the caudal fin. The pectoral, ventral, and anal fins are nearly colorless or light yellow; the second dorsal has fine dashes of brown and yellow arranged in irregular longitudinal rows. The first dorsal has more distinct colors in the breeding season when the outer margin is of dull grey with an irregular

yellow bar beneath; a row of oblique brown dashes separates this from the grey of the lower half of the fin.

The young males are described (Jordan and Everman, 1896) as variously marked. Those sexually immature look like the females. The fully developed males, when not breeding, show the general pattern already described for the females but have the transverse bars on the posterior part of the body of bluish tint and have pale reddish orange spots between these. Varying amounts of peacock blue may be found on the cheeks and the ventral, anal, and caudal fins. The second dorsal is made conspicuous by two broad bands which extend the length of the fin;

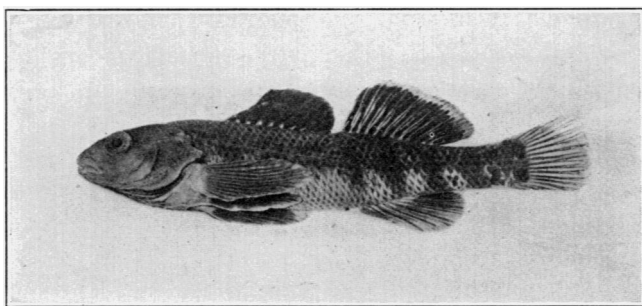


FIG. 1. The male *Etheostoma caeruleum* Storer, as he turns to display his ventral fins to another male. Photograph of a living fish slightly retouched.

the upper is of dull brick red while the lower is of peacock blue. The first dorsal is much like that of the female but with colors more intense since peacock blue takes the place of the dull grey of the outer margin. Over the belly and throat are patches of salmon or pale orange.

According to Jordan and Everman (1896), this *Etheostoma* is a Mississippi Valley form and the most abundant darter of the Ohio Valley. During most of the year these fish lurk among the stones and gravel of the small streams they inhabit. Their habitat is swift water. They are found at the lower ends of the rapids where the water enters the pools along the course of the stream, and also among the stones of the rapids themselves.

Living thus in exposed places the darters are very alert. If one approaches the stream cautiously, so as to remain concealed

until close to the edge of the rapids, he may see the startled fish flee by quick short dashes and sudden turns, and then they disappear. By carefully examining the bottom they may now be found lying in sinuous curves on the gravel or nearly hidden under the edges of stones with only a small part of the head or tail in sight. Here they pose at any angle to the current. They are often seen peering among the stones for food while supported on the pectoral fins so that the head and front part of the body are lifted above the bottom. The large pectoral fins are used both for progression and in directing movement. The second dorsal is usually elevated and with the anal presents a broad surface to the water when the tail is used in swimming. This very likely helps in their rapid, jerky, forward rushes which more resemble the leaps of a cricket than the graceful movements of a fish. The sudden darts and quick turns may serve to confuse an enemy, and to allow the fish to make off. But when no shelter is available the darter assumes a death-like quiet, and is then nearly invisible on the gravel bottom.

The shyness of the *Etheostoma* was shown when a number were brought into the laboratory and placed in an aquarium. For weeks they would not eat while observed and when any one was near they lay motionless upon the bottom. In time they learned to come at once to the side of the aquarium when I approached to feed them. But even after six months they fled as though frightened when a stranger came near or when I appeared in light colored clothing to which they were not accustomed. They seem to be capable of as much discrimination as the dace (Washburn and Bentley, 1906), but like young *Necturus* (Whitman, 1899) they are extremely timid so that it is a long time before they show their intelligence by their behavior.

III. THE BREEDING COLORS, HABITAT AND BEHAVIOR.

With the coming of the breeding season¹ a change takes place in the rainbow darters as to color, habitat, and activities. As stated, the females retain their usual colors. They are somewhat

¹ The breeding this year (1906) was observed from April 24 to June 2. It is probable that the season began before my first records, as the males in the brooks had their bright colors the second week in March.

darker than later in the season, but are inconspicuously mottled with dark colors on an olive or brown background. In the young male the first dorsal often shows a dark blue color, the first bright color to appear. But the breeding males (Fig. 1) take on brilliant shades of red, orange, blue and green. As Holt (1898) states for *Callionymus*, so also in the male of *Etheostoma*, the back retains its mottled brown appearance, while the color pattern of the sides and fins becomes very brilliant. The blue of all parts becomes more intense and is of a bright peacock shade except where apparently darkened by black as in the bars and the ventral fins. The reds also become in places a bright orange. The most brilliant colors were observed the first part of the season. Besides these seasonal changes, there are many individual variations. The blue of the first dorsal may cover the whole fin so as to obliterate the pattern. The blue bands across the posterior part of the body may be six or four instead of five; the red which alternates with these may form intervening bands or may occur in patches above and below the lateral line; the caudal fin which is sometimes light greenish blue may have two pale red or yellow lines radiating from the base of the fin. In addition to individual variations and seasonal changes there are changes in color tone which occur from day to day or from moment to moment. (1) The ground color in both sexes varies in tone with the color of the bottom. Thus it is dark on an ooze covered bottom, but when the high water sweeps away the ooze and exposes the underlying yellow sand the color of the fish becomes lighter in harmony with the bottom. (2) The colors are more brilliant when the temperature of the water is low. This change of color with decrease of temperature does not appear to coincide with increased spawning activity, since spawning was not observed when the water was below 15° C. The brilliant colors coincide rather with the low temperatures of the early part of the season before the actual spawning. Besides this the brilliant colors of the males, especially the blues often flash out momentarily and fade again when the rivalry between them is most intense, as described below.

In the spring the darters leave their lurking places in the rapids and congregate on the gravel sheets which are spread out at the

head of the rapids where the stream leaves a pool. Here the water is from one and one half to four or six inches deep with a current moving at the estimated velocity of about 75 feet per minute. The pebbles of the bottom are small, averaging one half inch in diameter while the largest is not over two inches. As these gravel sheets are the areas used by the dace (*Semotilus atromaculatus*) and stone-rollers (*Campestris anomalum*) in nesting, the ground is often roughened by their pits and ridges.

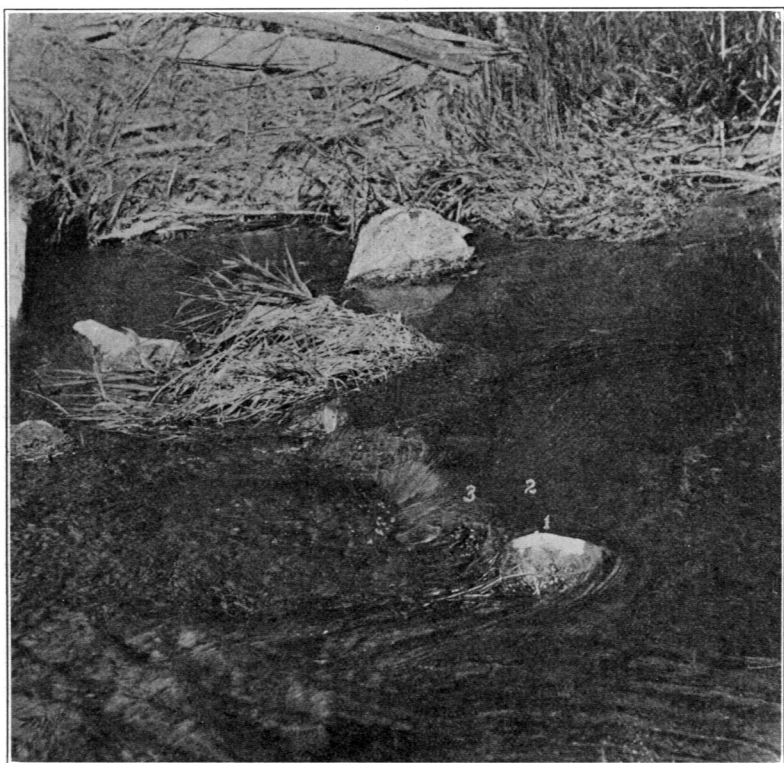


FIG. 2. The breeding ground of *Etheostoma caeruleum* Storer. The stream is here about six feet wide. The stone at 1. is about a foot long. The numbers indicate the holding of fish "A."

The change in the behavior of the darters is as marked during the breeding season as the change in color or habitat. While the fish are at other times shy, rushing for shelter on one's ap-

proach or lying so still as to escape notice, they now make no effort at concealment. It is often possible by nearing the stream slowly to reach the margin without frightening them. They quickly become accustomed to one's presence and are then not disturbed by one's wading among them. I have touched them with my boot tips or stroked them with a small wire without their moving. It is then possible to stand directly over them and even to examine them with a hand lens without in any way modifying their normal behavior. They appear to swim here and there at random.

The breeding areas so swarm with them that, one day, I counted twenty-six in a single square yard. Since the females are so inconspicuously colored as to be easily overlooked, there may have been more fish in that space. There always seemed to be more males than females present on the spawning ground. Early in the season I estimated four or five to one, and among my notes for June 1 is the item, "Seven darters in sight ; only one female." This proportion continued for several days but collections of fish made in November did not show this inequality in the number of the two sexes. It therefore appears that the larger number of males on the breeding grounds depends on the difference in the habits of the two sexes as is shown below.

IV. THE SPAWNING.

Although all the fish seem to be moving about over the spawning area promiscuously, close watching shows that this is true only of the females and small males. On the other hand, there are some of the large brilliant males which remain each within a restricted area which he guards and from which he drives the other males. Among such males it often happens that a single individual may be distinguished by peculiarities of coloration and may thus be kept under observation for hours at a time. The plots guarded by individual males we may call their "holdings." The width of these holdings does not usually exceed fifteen inches but as the length varies from fifteen inches to two feet they may include more than two square feet. A male may leave his holding to pursue a female or he may go beyond it while he energetically drives away another male, but in either

case he immediately returns. Each spawning area has a number of such holdings guarded by the large males.

1. *Behavior of a Large Male toward a Female.*

When a female enters the holding of a large male it rarely happens that the two are left undisturbed. Usually their behavior is greatly complicated by the interference of other males, but for the sake of clearness we may first consider what happens when the two fish are left undisturbed.

The female usually swims into the holding from below. The male then approaches her from behind as she lies on the bottom with her head up stream. He often places himself behind her, his body parallel with hers and with his snout touching her side near the posterior margin of the first dorsal. While in this position he may move his head with a trembling, vibratory motion. This vibration appears to have a rate of from four to eight per second and must cause a gentle tapping of the side of the female. The male may now move away from the female for some inches and upon returning, may place himself above the posterior part of her body and may then again move off for two or three inches and return. He becomes ever more excited in his movements and may at times place himself at right angles to the female an inch or so from her head and then vibrate his pectoral fins and head and elevate his gill-covers somewhat more than usual. This is not a very frequent mode of behavior but it may serve to display the colors of his cheeks, opercula and throat to the female. At any time the female may withdraw a few inches to one side. Once I counted ten such successive side-wise moves by a single female, each of two to four inches. The male followed after each move; sometimes he came near enough to tap her side, while at other times he lay at a distance — not exceeding three inches — and seemed to watch and to wait. If disturbed, as she sometimes is, by the vigorous taps or pokes of the male, the female may swim off for a few feet. To do this she often drops back and to the side, then turns and dashes up stream. She may thus escape pursuit by the male. On the other hand if the female starts directly forward while the male is near he follows very closely, since he appears to interpret the forward motion as the sign that

she is preparing to take the position for spawning. This whole process of stimulation by the male is manifestly adapted to excite the female to the spawning act.

2. *The Spawning Attitudes.*

When the female is ready to spawn she lowers her head and with her long axis at an angle of about 45° to the bottom she drives herself forward by vigorous strokes of the tail. This sends her head into the gravel. When she has succeeded in burying her head and the anterior part of her body beneath the gravel she depresses her tail so as to bring her long axis parallel to the bottom. This brings her head above the bottom but leaves her pectoral fins and the ventral portion of her body buried in the sand or gravel. The pectoral fins are extended at right angles to the body and add to the surface that is under the sand; they thus form an anchor which prevents the current from displacing the fish while the eggs are being deposited. If, either by the action of the water or by the movements of the males along the

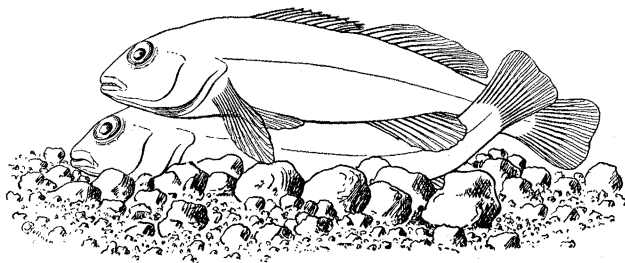


FIG. 3. Spawning attitude of *Etheostoma caeruleum* Storer, at the beginning of the act. Drawn by Mr. Carl Kellner from sketches by the author. Natural size.

sides of the female, her pectoral fins become uncovered; or if she is not successful in covering them when she attempts to bury herself, she moves a few inches trying again and again until her pectorals are fully covered. When the female has thus partially buried herself the male, recognizing her readiness to spawn by her behavior and attitude, may at once place himself above and parallel with her as she lies half-concealed in the sand (Fig. 3). His ventral fins are extended along her sides and rest against her body just in front of and below her first dorsal. His pectorals

are held nearly at right angles to his body often with their lower margins on the gravel. His anal fin is extended on one side of the female close against her body while his caudal fin is applied to her tail on the side opposite his anal. The position of the male is largely maintained by the firm hold given by pressing his ventral fins against the rough ctenoid scales of the female, while the backwardly directed spinules on his scales hinder his slipping backward and the spinules on her scales keep him from slipping forward. The crossing of the tail of the female by that of the male is frequently not maintained during spawning but seems to be the means by which the motion of the two fish is started in unison.

3. *The Spawning Act.*

When thus placed (Fig. 3) the male vibrates the head in the agitated trembling manner already described. This seems to be a stimulus for the spawning for usually the two fish begin at once a movement of the posterior portion of their bodies from side to side in unison. The motion is a very rapid vibration through only a short distance and lasts for several seconds. During this time the sand and gravel are stirred up and make a cloud which partially obscures the fish. At the same time the caudal fin of the male slips over that of the female so that it is on the same side of her body as his anal. That the eggs and milt are extruded at this time was proved by picking up the fertilized eggs immediately after the spawning had taken place. The eggs are adhesive and remain sticking to the gravel which forms the bottom of the depression in which they are deposited. Here they were found a number of times with the help of a reading glass, and were scooped up with the gravel in a bacteria dish and were found to be identical with those obtained by stripping the female. They are spherical, and measure about 1.5 mm. in diameter. They are pale yellow in color and contain a large oil drop. Only from one to six eggs were obtained at one time by stripping the females, but large individuals deposit probably twice or three times that number. Although the milt is of a milky color it is not shed in sufficient quantity to be seen in the cloud of sand stirred up by the rapidly moving fish.

Spawning may be repeated a number of times before the fish separate. Sometimes during spawning the fish, without separating, move forward along the bottom for short distances. In such cases, or whenever the anchoring of the female has yielded so that she is moved from the bottom by the vigorous activity of the two fish, she leaves the spot where she was lying and again buries herself before spawning is repeated.

4. *Behavior of Two Rival Males toward Each Other.*

Since the fish are crowded into small areas during the season of sexual activity, it is rare for a pair to spawn without a number of males crowding about the female. When a female enters the holding of a brilliant male, several males may attempt to follow her. As one of them approaches, the owner of the holding raises his first dorsal which is a very dark brilliant blue. Often at this warning a small male at once retreats, but if the fish are nearly equal in size and coloration the new comer may stand his ground and also make a display of his colors. With his first dorsal displayed by extending it until its anterior margin rests on his back and points forward, the defender of the holding may then turn on his long axis until his ventral surface is visible to his rival. He thus shows off its dazzling orange and the deep blue of the ventral fins. This attitude is shown in Fig. 1. While he is thus posed the two males frequently move to positions close to the female and parallel with her but on opposite sides. During this display the blue of the cheeks and ventral fins frequently flashes out and becomes darker. This momentary intensification of color was more noticeable early in the breeding season than toward its close.

If the intruder does not retire after this brilliant display he receives a series of blows administered by the defender of the holding who swims at his rival and strikes him repeatedly one fourth to one half inch back of the opercular region. Sometimes the blows are given by swimming directly into the opponent and using the head as a weapon, at other times by swimming past close beside him and giving a swift stroke of the tail. These combats from all appearances are as harmless as the color display but are in the end always successful in driving away in-

truders. They may be called sham combats. Occasionally the intruder resists. Then the two males range alongside each other, depress their heads nearly to the bottom of the stream, and with that peculiar trembling motion of the head already mentioned, and with synchronous movements of their caudal fins, swim about here and there side by side or move side-wise across the stream for short distances. The rivals when thus engaged rarely swim forward from the holding yet I have once seen two males swim forward for some ten feet, moving the caudal fins in unison while keeping so close together as to seem to touch one another. Professor Reighard tells me that he has observed a similar form of behavior to be habitual with horned dace (*Semotilus atromaculatus*).

5. *Behavior of Supernumerary Males toward the Spawning Pair.*

Young males frequently follow the female as she moves about in the breeding area. They approach, as already described, and tap her side; they often move forward so that the tapping is near her head. When thus disturbed the female swims off for a number of feet but does not often escape the small tormentors who swim up beside her and continue their vigorous stimulation. They are more agitated in their behavior than the larger males, especially during the latter part of the season. As the large male guards the female in the holding these young males often surround the pair. They lie off at a distance of six to eight inches and make frequent attempts to approach while the male in the center keeps up a nearly continuous chase to drive them away. During the spawning they often swim close to the side of the female moving the gravel from near her as they wedge themselves in at her side. When a number are present they may entirely cover the pairing fish. During the spawning the small accessory males that are in contact with the spawning pair move the body with the same vibratory motion and thus appear to take part in the spawning. They are not brilliantly colored. An examination of the milt showed them to be nevertheless mature. The spermatazoa were as active and when mounted in water their movements were as long continued as in the case of large, brilliant fish.

6. *Sex Recognition.*

Sometimes when a female slips out of sight of the male that has been guarding her, he, seemingly unaware of her absence, approaches a small male as if he mistook him for the female. As he approaches the young male the latter sometimes raises his lightly colored first dorsal as if to show his identity and then usually flees. In this case the large fish apparently fails to discriminate between the light-colored male and the female.

This failure was especially apparent in one instance when several males rushed from various distances and directions toward a young male that happened to burrow into the sand while feeding and thus took nearly the position of a female preparing to spawn. None of the males followed the young male as they would have followed a female, nor did they feed when they came near the spot where he had been, as they would have done if their approach had been due to the suggestion of food by the attitude of the young male. It thus seems probable that at a little distance the male fails to distinguish between dull males and females. The more nearly the behavior of a dull male simulates that of a female, as in the case of the male burrowing for food, the more is he likely to be mistaken for a female. Upon the near approach of the brilliant male the young male erects the first dorsal and rapidly escapes, modes of behavior not observed in the female. It appears then that the brilliant fish distinguishes between the two by their behavior; a mode of sex recognition pointed out by Holmes (1903) in the case of amphipods. In the case of very young males the sex recognition must be wholly of this character, while males which already show some little sexual coloration are probably distinguished upon near approach by means of it as well as by behavior. Holt (1898) believes that a similar method of recognition occurs in the dragonets.

V. OBSERVATIONS BEARING ON SEXUAL SELECTION.

The preceding description of the breeding activities of the rainbow darters at once suggests that a field study of their behavior may be made to yield evidence as to the occurrence of sexual selection among them. The fish are crowded together in the breeding areas; the sexes are easily distinguishable; they may

be readily observed under wholly natural conditions ; the breeding season is brief. Here if anywhere under field conditions it should be possible to determine whether sexual selection occurs.

I therefore attempted to observe continuously for as long a time as possible the behavior of individual fish in order to learn whether the more brilliant males succeed in spawning more frequently than those less brilliant, and whether individual females spawn more frequently with brilliant males than with those less brilliant. Individuality in color pattern has made it possible to thus follow and identify individual fish for several hours continuously. I have further noted in a large number of cases the colors of the pairing males in order to learn whether the more brilliant males are successful in a larger proportion of cases than the less brilliant males.

From a number of records in my notebook I have selected three of individual fish, that of a brilliant male (*A*), of a dull male (*B*) and of a female (*C*). An extract from my field notes of May 18, 1906, gives an average picture of the movements of a large male (*A*) that was under continuous observation for the latter half of the afternoon of that day. He had his holding on a gravel area just above a tiny rapid. The rapid was made by large stones and débris which obstructed the course of the stream and formed the lower margin of his area. Fig. 2 shows the breeding ground of this fish.

Fish A (Male).

4:05 P. M. A female is in the area with *A*. There is spawning.

4:10. Spawning is repeated ; a small male rushes in beside the two fish. The female swims away with the small male while *A* remains near the spot marked No. 1 in Fig. 2.

4:13. *A* withdraws about a foot and begins to fight a male of his own size ; both display their dorsal fins.

4:15. *A* is back at No. 1.

4:15 ½. He moves away less than a foot to where a female is lying. Spawning again 8 inches from the first place (No. 2 in Fig. 2). The female remains quiet while he drives off intruders.

4:18. She goes away with a smaller fish that rushes in by her side and pokes her. *A* remains near No. 2 and seems to be feeding.

4:19. The female returns.

4:19½. A small male rushes up to the side of the female. He pokes her so that she swims off but not far. *A* remains.

4:22. He moves about eight inches to where a female is lying. The two are under a riffle so they cannot be seen distinctly. (This spot is No. 3, Fig. 2.)

4:22½. *A* drives off a male.

4:25. He is guarding the female : he spreads his fins at the small male present at 4:19½. The female swims away and several males which have been near follow close after her.

4:27-30. *A* guards the holding.

4:31½. He seems to eat something near No. 2. He turns his head and searches quizzically among the stones.

4:34. Another female comes in but a small male is pursuing and she does not stay.

4:36. The female appears from under the riffle at No. 3 and buries herself as for spawning.


4:38½. She remains quiet while he guards her.

4:39. She moves to a spot in line between No. 2 and No. 3.

4:41. He drives off other males from the female for a space of a foot.

4:42. The spawning activity is begun but the female moves away and it is not completed. After this for several minutes no females are in sight. *A* moves about and once, when near No. 3, seems to feed and then he seems to spit something from his mouth.

4:51. A female slips into the area from below.

4:52. *A* approaches from behind and touches her side, while the two fish are in the following attitude .

4:54. Spawning occurs ; a small male tries to crowd in beside the female ; she moves and leaves. *A* remains, guarding the spot where spawning has just occurred.

5:05. The female again enters and buries her head and the ventral part of her body. She is between No. 1 and No. 3. *A* drives away a small male.

5:08. He moves up to her head and seems to display himself to her. He drives away a small male.

5:10. She tries again to bury herself. *A* comes close to her, tapping her side.

5:11. She tries again to bury herself, again he taps her side in position here shown ($\begin{smallmatrix}) \\ A \end{smallmatrix}$).

5:12½. She buries herself, but again goes off and two small males follow her as she swims to a point some three feet away while *A* remains.

During the last twenty minutes of the above record the same female was under observation and it is probable that the same one was in the area earlier, but watching the male made it impossible to follow the female in each case. This brilliant male rarely left an area approximately two feet long and eight or ten inches wide. During the first hour there were in this area but four spawnings, in all of which this male took part. A comparison of his activities with those of a small dull male is instructive.

Fish B (Male).

After choosing an especially small, dull specimen the following notes were made, on May 22 :

3:12 P. M. *B* is in area *X* (about a square foot in the center of the stream which looks like a favorable spawning area, and is a point from which to measure his movements).

3:14. *B* moves down stream for a short distance toward a female which is approaching *X*.

3:15. He is back in *X*.

3:15½. *B* moves toward the side of the stream and follows a female, but a large brighter male remains near her.

3:17. *B* is again in *X*.

3:18. *B* moves two feet back and to the side.

3:18½. *B* is in *X*.

3:21 P. M. He is driven away from *X* by a small but brighter male.

3:23. *B* moves out to the side 18 inches, then one foot in front of *X*; next 18 inches to the side of *X*. Every male seems to drive him away.

These records extend to 3:37½ and show continuous movements by *B* every one half to two minutes and extending in

every direction from *X* and over distances of from four inches to four or five feet. He raises his first dorsal occasionally as he is driven about. It seems possible that at a distance the other males mistake him for a female. While there is in the case of this male no record of spawning, notes of other days observations show that the small, dull males succeed occasionally in spawning. They sometimes rush into an area guarded by a brilliant male and spawn with the female, while the brilliant male is chasing away other intruders. They also often move close to the female and into the mantle of males which covers her while she is spawning. Yet relatively few times are these small males successful in spawning.

Fish C (Female).

From my notes of the afternoon of May 12, when watching a single female, I give a sketch of the hour from 4:15 to 5:15. At the beginning of this time a small, dull male poised near a female gave her four to six taps with his lower jaw just back of her first dorsal. She started to bury herself, then two bright males came, she moved forward about 18 inches, followed by a brilliant male with which she spawned after burying herself. A little later followed by a dull male she came near a brighter male and he pursued her for about two feet. A dull male came and tapped her side. She started and moved quickly forward and to the side two or three feet to where there was a large brilliant male. He drove off the small males, she buried herself and the two spawned. Two other males crowded in at her side during the spawning. After spawning the fish were quiet for a few moments when the female moved to the shelter of a stone and remained quiet about one half hour. She then moved to the opposite side of the stream and was quiet again. At the end of the hour a small dull male tapped her side, she moved forward, buried her pectorals and a medium sized dark colored male spawned with her. Thus in a single hour this female spawned three times, each time with a more brilliant male, while during the same period three attempts of small or dull males to spawn with her were frustrated at their beginning.

These are samples of the records of individual fish. I also

made a note of the pairings observed and in 57 cases recorded the color of the male. These results are arranged in the following table.

TABLE SHOWING THE COLOR OF THE PAIRING MALES IN FIFTY-SEVEN SPAWNINGS OF *Etheostoma caeruleum*.

Color of Male.	Number of Records from April 24 to May 18 Inclusive, 25 Days.	Number of Records from May 19 to June 2 Inclusive, 15 Days.	Whole Number of Records.	Per Cent. of the Whole Number.
Bright.	17	18	35	61.4
Medium.	3	5	8	14.0
Dull.	2	12	14	24.6
Total.	22	35	57	100.0

The largest males and many of the somewhat smaller ones are bright colored and are classed as bright. Others of the smaller males are not so bright and are classed as medium; the small fish with little color are classed as dull. If we divide the medium class between the bright and dull we have a ratio of 39 bright to 18 medium and dull or a percentage of about 68 to 32. This is perhaps as fair a statement of the results as can be made. The work, however, does not furnish conclusive evidence of selection because the results are complicated by the presence of supernumerary males. In 17 of the 35 cases recorded in the table for bright males there were from 1 to 6 of the smaller fish present. Though it is probable that they are less effective in the fertilization of the eggs than are the bright males, they cannot be neglected in the consideration of the problem. This is more evident from the fact that the brilliant males rarely take a position among the supernumerary ones. The table shows that the small males succeed more frequently toward the close of the season than at the beginning. If it were true that only the larger females spawn the first of the season then it would be relatively sure that there was selection by the pairing during this time of the larger and better developed fish of both sexes, but this is not the case because among the very first day's notes is the statement that the females spawning varied in size from those only about one third the size of the large males to those as large as the average fish. In spite of these disturbing factors, the larger percentage of cases in

which the brilliant males are successful, the fact that they are the largest and most vigorous and the advantage which results to them from their position during the spawning act, makes it probable that much the larger part of the eggs are fertilized by them.

VI. DISCUSSION OF RESULTS.

1. *Origin of Nest-Building Habits.*

The facts here presented show clearly that certain large males have holdings which they guard and over which they remain, while the females and young males are moving about in the breeding area. The way in which these areas come to be held by the large males was not observed, but it seems possible that the result has been reached in the following manner: As the female moved about at the beginning of the season with the males following her, she attempted to bury herself, but owing to the hardness of the bottom was at times unsuccessful. She repeated her attempt until she came to a place where the bottom was loose, and where she easily worked herself into the gravel (*cf.* for Salmon, Rutter, 1903). Then spawning took place. When she moved she again succeeded in burying herself where the sand was loose. Since the large males were able to drive away the smaller ones, they appropriated to themselves those areas within which the bottom was of a character suitable for spawning. These were their holdings. When a male had once taken possession of a holding he received into it a succession of females and guarded it continuously against the intrusion of other males. In this way he not only secured to himself the successive females that visited his holding, but incidentally he guarded the eggs that had been deposited in it and prevented their being eaten by the females and by other males. By this method the breeding area may have come to have a number of holdings, each defended by its male.

In *Etheostoma* the male does not in any way prepare the holding for the reception of the eggs, but these are laid here and there at random wherever the bottom proves suitable. There is in this case no real nest. It has been noted that among certain fish which do in one way or another prepare a nest for the eggs, an

area of the bottom surrounding the nest is guarded (Reighard, 1903 and 1905) and so may be considered the holding. Thus the habit which the male of *Etheostoma* shows of guarding a limited area of the bottom may be regarded as more primitive than that of the nest-building fishes. It represents probably a stage in the evolution of the nest-building habit.

2. *Displays of Color and of Movement.*

There is a marked difference in the behavior of the males and females on the breeding area. The females are passive and, save as they swim off to avoid the males that crowd about them to stimulate them with their vibratory tapping, they make no response to the solicitation of the male, no displays of color and no responsive movements. Only once have I seen a female respond by a trembling movement of the head and pectoral fins. In all other cases the females appeared indifferent to the fish about them. In contrast to this is the behavior of the males. The large, brilliant males make less use of mechanical stimulation than do the smaller ones. As has been stated the larger males sometimes remain quiet at the side of the female for a considerable time while only a few inches distant and in full view. Occasionally one places himself at right angles to a female and, with his head about an inch from her's, elevates his gill covers and vibrates his pectoral fins. Whether either of these attitudes is for the purpose of displaying to the female the colors of the male is not easily determined. The younger, less brilliant males have never been observed to make any display of color and appear to rely wholly upon mechanical stimulation. They are more active than the older males and follow the females more persistently so that the vigor of movement shown by the males in courting may be said to vary inversely with the brilliancy of their colors. The rate of the vibratory movement of the head of the male has not been measured but was compared with the rate of the most rapid tapping which could be made by a slight movement of the fingers and was then estimated at from four to eight per second. As the lateral line organs are sensitive to such vibrations (Parker, 1903) it is possible that when the fish are not in contact the vibratory movements of the male are transmitted

through the water and affect the lateral line organs of the female. In any case it appears that mechanical stimulation forms the chief element in the behavior of the male toward the female while attitudes especially suited to display his colors are less evidently used.

Between the males color displays are frequent. If two brilliant males are rivals and of the same size they pose side by side with their first dorsals elevated. If one of the two fishes is a small male he does not pose, but after elevating his first dorsal flees. This display by the small male appears to serve as a sex recognition character by which the other males distinguish him from the females. Displays of force also take place between brilliant males. These consist of blows delivered by the tail or head of one male against the side of the other. Or they consist of sham struggles during which the fish swim about side by side. While thus swimming the first dorsal fin is always raised and each of the two fish makes use of the same vibratory movement of the head that is used toward the female. The net result of these displays of color and force between males is in the majority of cases to exclude the smaller males from participation in pairing. They appear to have, however, a further effect; that of raising the general state of excitation among the males. H. E. Zeigler is quoted by Gross (1896) as expressing the belief that a high state of nervous excitement is necessary for the pairing of all animals. Häcker (1900) has applied this interpretation to the displays of color and movement of male birds during the mating season. He believes that they serve to overcome the coyness of the female and to bring her into the physiological state necessary for pairing. The same interpretation seems to apply to the breeding behavior of the male *Etheostoma*. Were the displays of color and of force of the individual male merely random, not manifestly adjusted to a female in one case and to a male in another case, then they might be interpreted as the meaningless result of nervous excitation. But since they are exactly adjusted I conclude that they have, in addition to their function of limiting the breeding activities of the smaller males, a further definite function; that of raising the general state of excitation among all the participating fishes.

3. *Sexual Selection.*

The evidence has been already presented to show that in *Etheostoma* the bright males are most frequently successful in spawning. I would be justified, from some days' observations, in claiming evidence for sexual selection in the Darwinian sense, a selection of the brilliant males by the females. For my notes show that the females, although followed in their course by small males, often go directly from the holding of one large male to that of another. They thus appear to consciously neglect or repel the smaller and more insistent males and to give preference to the larger ones. On the other hand my observations show that the females spawn with whatever male happens to be present. Even in the holding of a large male the spawning is sometimes with a small one while the large one is driving away intruders. Hence, although the brilliant males are more successful in pairing than the duller males, yet I find no evidence that the female *chooses* them. What appears to be a choice of males is probably in reality a choice of spawning places. This subject has been discussed under the heading "Origin of Nest Building Habits." We then find no sufficient evidence in the behavior of the female that she so discriminates between males as to give to any color or color pattern selectional value in the sense of Darwin (1883). If this be true, the displays of color and movement (by the male before the female) result, not in a selection by the female of particular males but only in an increase of the general state of nervous excitement among the participating fishes. (Cf. for birds Häcker, 1900.) It does not appear that the female exercises any choice either conscious or unconscious based on color or movement.

The only form of selection that appears to be present is that which arises from the rivalry of the males and results in the limitation of the breeding activities of the smaller males. Since the smaller males undoubtedly breed when older the case is merely one of "seniores priores." The preponderance of the older males in the breeding cannot have resulted in the evolution of secondary sexual characters. This could have come about, by selection, only through the preponderance in the breeding of males having certain secondary sexual characters not possessed by other males.

It would seem that the more brilliant colors are of value to the males possessing them during their combats with other males. But whether the males that succeed in breeding really differ in any definite way in color or color pattern from adult breeding males in general, whether they belong to some one of the many types of coloration, my observations do not show.

SUMMARY OF OBSERVATIONS.

1. In the adult *Etheostoma caeruleum* the two sexes are distinguishable at all seasons of the year because the males have some red and blue in the color pattern while the females are mottled brown.

2. They usually inhabit the rapid water of small streams.

3. Out of the breeding season the fish are shy and not easily approached.

4. The breeding season was observed to extend from April 24 to June 2, 1906.

5. The sexual activity of these darters is limited by temperature and actual spawning was not observed when the water was below 15° C.

6. The colors of the larger males are more brilliant in the breeding season than at other times. The red and especially the blue are greatly intensified and appear on parts of the body on which they are not found during the rest of the year. The adult males show many variations or types of coloration.

7. The most brilliant colors were found the first of the season, or the last week in April.

8. The fish at this time congregate on the shallow gravel areas above the rapids.

9. They lose their shyness and allow close observation without showing signs of fear.

10. The sexes occur in equal numbers but there are always more males than females present on the breeding ground at one time.

11. Among these males certain large brilliant ones have holdings which they guard. They may leave these to drive away other males or pursue a female but they return promptly.

12. The driving away of rival males is by means of display or by blows of the tail or head.

13. The males occasionally display their colors to the female.
14. The males also tap the sides of the female by a trembling vibratory motion of the head.
15. Before spawning the females partially bury themselves with their pectoral fins covered by the sand or gravel of the bottom.
16. The male places himself above the female in the position shown in Fig. 3, and during a rapid synchronous vibration of the tails of the two fishes the eggs and milt are extruded.
17. The eggs remain adhering to the stones of the bottom of the very small depression made by the body of the female.
18. The spawning is frequently repeated by each female but only a few eggs are deposited at one time.
19. One or several males may be present during the spawning act.
20. When supernumerary males are present they take positions above the female and at her sides.
21. Large males seem to mistake the undifferentiated males for females and to distinguish them by behavior rather than by appearance.
22. The raising the first dorsal as practiced by the males seems to serve as a sex recognition character.
23. The brilliant males were successful in pairing in over 60 per cent. of the observed cases. The less brilliant males were thus excluded from the pairing in these cases, though they may have been present as supernumerary males.

MANISTEE, MICH.,

September 17, 1907.

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